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RESEARCH PAPER

Forest structure, productivity and soil properties in a subtropical evergreen broad-leaved forest in Okinawa, Japan

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Abstract: Structure, species composition, and soil properties of a subtropical evergreen broad-leaved forest in Okinawa, Japan, were examined by establishment of plots at thirty sites. The forest was characterized by a relatively low canopy and a large number of small-diameter trees. Mean canopy height for this forest was 10 m and stands contained an average of 5400 stems·ha^{-1} (≧ 3.0 cm DBH); 64% of those stems were smaller than 10 cm DBH. The total basal area was 54.4 m^{2}·ha^{-1}, of which *Castanopsis sieboldii* contributed 48%. The forest showed high species diversity of trees. 80 tree species (≧ 3.0 cm DBH) from 31 families was identified in the thirty sampling plots. *C. sieboldii* and *Schima wallichii* were the dominant and subdominant species in terms of importance value. The mean tree species diversity indices for the plots were, 3.36 for Diversity index (H´), 0.71 for Equitability index (J´) and 4.72 for Species richness index (S´), all of which strongly declined with the increase of importance value of the dominant, *C. sieboldii*. Measures of soil nutrients indicated low fertility, extreme heterogeneity and possible Al toxicity. Regression analysis showed that stem density and the dominant tree height were significantly correlated with soil pH. There was a significant positive relationship between species diversity index and soil exchangeable K^+, Ca^{2+}, and Ca^{2+}/Al^{3+} ratio (all p values <0.001) and a negative relationship with N, C and P. The results suggest that soil property is a major factor influencing forest composition and structure within the subtropical forest in Okinawa.

Key words: diversity index; evergreen broad-leaved forest; species composition; soil nutrient; soil-vegetation relation; subtropical zone

Introduction

Evergreen broad-leaved forests dominated by evergreen oaks (*Castanopsis* spp., *Lithocarpus* spp. and *Quercus* spp.) are widely distributed in the warm-temperate and subtropical zone in eastern Asia (Kira 1991; Song et al. 2005). The Ryukyu Islands, located in the subtropical zone (between latitudes of 30˚N and 24˚N), have native forests that are dominated by *Castanopsis sieboldii* with a high diversity of tree species (Suzuki 1979). On Okinawa Island, there remain well-developed stands, particularly at the northern part (Miyagi 1990; Itô 1997). The basic feature for this forest is low canopy with a dense understory and high diversity of tree species (Itô 1997; Xu et al. 2001). We are unaware of any study that has documented the relationship between soil properties and forest composition and structure in this area. If repeated disturbance is the primary factor for development of this peculiar structure for the Okinawan subtropical forest, then one should find a relatively weak relationship between forest vegetation and soil properties. The present study is aimed at determining the extent to which soil properties influence forest composition and structure in the Okinawan subtropical forest.

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Study area and methods

Study area

This study was conducted in the northern part of Okinawa Island, southwest Japan. The area is characterized by a subtropical climate and abundant rainfall throughout the year. Annual mean temperature is about 21.8ºC, and the mean extreme temperatures in the coldest month, January, and the hottest month, July, are 5.4ºC and 34.5ºC, respectively. Annual mean rainfall is 2 680 mm (Experimental forest, University of the Ryukyus). Typhoons frequently occur between July and October, bringing high rainfall and strong winds to the island. Monsoon, from the south or southwest, brings a rainy season between spring and early summer, and from the north or northwest creates a relatively dry season in winter.The topography of the area is mountainous with the highest peak, Mt. Yonaha of 498 m a.s.l.. Deep valleys dissect the area and steep slopes predominate. The bedrock is com-

posed of tertiary sandstone and palaeozoic clay-slate except for a narrow area of palaeozoic limestone along the coastal line, and a yellow soil has developed (Kojima 1980). This soil type corresponds to Typic Paleudults in the USDA classification (Cultivated Soil Classification Committee 1995).

The mountainous landscape is covered with orange plantation and a wide range of forest ecosystems. The majority of Okinawan subtropical forest is dominated by a secondary forest that has been harvested for fuelwood, particularly for charcoal production during the World War Two; most of the lower slopes once covered by subtropical forest also have been converted to orange and pine plantations (Yamamori 1979). This subtropical forest is characterized by short canopy with a dense understory (Xu 2002).

Vegetation survey

A total of 30 plots with an area of 20 m × 20 m in size, were established in the forest stands which have been undisturbed by human activities at least since World War Two. All trees with diameter at breast height (DBH) larger than 3.0 cm in each plot were numbered, and identified to species. Their DBHs were recorded. Height was estimated for all trees using a 12 m drawing pole with scale.

Soil sampling and analysis

Soils were sampled and described by digging one or two soil profiles, each over 80 cm deep, in every sampling plot. Soil samples were taken from different soil horizons in every profile. Prior to analysis, samples were air dried, ground, and then passed through a 2-mm sieve. Soil pH was measured in a 1:2 mixture of soil and deionized water using a glass electrode. Organic carbon and total nitrogen were determined by dry combustion with a C-N Analyzer (Yanaco, MT-500, Kyoto, Japan). Subsamples of soil to be analyzed for phosphorus were extracted using the Bray Ⅱ method. Subsamples of soil to be analyzed for exchangeable K^+, Ca^{2+}, Mg^{2+}, Na^+, and Al^{3+} were extracted with 1 mol L^{-1} NH_4Cl solution (Meyer and Arp 1994). The above-mentioned elements were determined by inductively coupled plasma spectrometer (Shimadzu, ICPS-2000, Kyoto, Japan).

Data treatment and analysis

A combination of density, frequency and basal area is often used to measure the relative importance of a woody species in a forest community (Whittaker 1975). The plant frequency index depends greatly on sampling plot size (Crawley 1986) and is a useful index whenever the sampling covers a substantially large area. As our sampling plot size was relatively small, we used a combination of the relative basal area (RBA) and relative density (RD) of each woody species per sampling plot as the importance value (IV), which was estimated as:

$$IV\ (\%) = (RBA + RD) / 2 \quad \text{(Basnet 1992)}$$

Where RD (percent) was calculated by summing the number of stems of a species in a plot, dividing by the total number of stems of all species in the plot, and multiplying by 100. RBA (percent) was calculated in the same way using the basal area instead of the number of stems.

Three parameters of the plant community, namely species richness (S′), diversity index (H′) and equitability index (J′) were calculated for each sampling plot. S′, H′ and J′ were calculated according to the following equations (Pielou 1975):

$$S' = \log_2 S$$
$$H' = -\sum (P_i \cdot \log_2 P_i)$$
$$J' = H' / S'$$

where S was the total number of species occurred in each sampling plot; P_i was the importance value of the i th species.

To explore for any relationships between structure parameters and soil chemical properties, we used Pearson Correlation on the statistical package (Statsoft, Japan 1999). As recommended by ter Braak (1995), all structural parameter values were log-transformed (ln) to meet the assumption of normality before entering the analysis, as their distributions were skewed towards a few very large values. The accepted level of significance was $p < 0.05$. The nomenclature of species in the present paper follows Hatusima and Amano (1994).

Results

Structural characteristics

Subtropical evergreen broad-leaved forest in Okinawa was relatively low in stature. Mean canopy height was about 10 m, and 90% of the sample plots had canopy height less than 12 m (Fig. 1B). *Schima wallichii* Korthals and *Styrax japonicus* Sieb. et Zucc. occasionally reached a height of 18 m; *Persea thunbergii* Kosterm., *Lithocarpus edulis* Rehd., *C. sieboldii* and *Pinus luchuensis* Mayr. reached 15–16 m in height (Table 1).

Stem density (≧ 3.0 cm DBH) averaged 5 400 stems·ha^{-1} (Fig. 1C); and about 36 % of those stems were larger than 10 cm DBH. The mean DBH was 9.5 cm. The largest stems (> 40 cm DBH) were exclusively *C. sieboldii* (maximum DBH 83.0 cm), *Distylium racemosum* Sieb. et Zucc. (60.7), *S. wallichii* (50.3), *P. luchuensis* (48.3), *Myrica rubra* Sieb. & Zucc.(42.2), *Scheffera octophylla* Harms (41.3), and *Quercus miyagii* Koidz. (40.2) (Table 1).

The mean total basal area of stems was 54.4 $m^2 \cdot ha^{-1}$. Approximately 83.5 % of the basal area occurred in stems with DBH ≧ 10 cm (Fig. 1D). *C. sieboldii*, however, accounted for 48.4 % of the total basal area.

Floristic composition and tree species diversity

A total of 80 tree species (≧ 3.0 cm DBH) in 31 families was identified in thirty plots. The mean number of species per plot was 27 (Fig. 1A). The families that had the most number of species were, Theaceae (9 species), Symplocaceae (8), Lauraceae

(6), Aquifoliaceae (5) and Rubiaceae (5). 12 families (38.7 % of the total) had only one species in all sampled plots (Table 2).

Table 1. Important tree species with Importance Value (IV) of over 0.2 in Okinawan subtropical forest. Quantitative parameters: N, number of individuals; PN, number of plots; BA, total of basal area (m^2); D_{max}, maximum diameter at the breast height (cm); H_{max}, maximum height (m); IV, importance value (%). Species are ranked by descending IVs.

Species	N	PN	BA	D_{max}	H_{max}	IV
Castanopsis sieboldii Hatusima	1467	30	31.11	83.0	16	35.53
Schima wallichii korthals	426	30	8.34	50.3	18	9.78
Daphniphyllum glaucescens Bl.	471	27	2.68	34.8	11	5.72
Rapanea neriifolia Mez.	576	30	1.52	14.1	9	5.63
Distylium racemosum Sieb. et Zucc.	339	22	3.32	60.7	12	5.20
Elaeocarpus japonicus Sieb. et Zucc.	362	29	1.40	20.2	10	3.88
Syzygium buxifolium Hook. & Arn.	360	29	0.76	12.4	8	3.37
Ilex liukiuensis Loesn.	225	26	0.91	20.3	11	2.44
Meliosma lepidota Bl.	159	19	0.95	19.8	10	1.96
Schefflera octophylla Harms	116	18	1.15	41.3	14	1.79
Cinnamomum doederleinii Engl.	145	23	0.80	30.1	12	1.74
Rhaphiolepis indica Lindl.	155	22	0.60	17.1	11	1.66
Persea thunbergii Kosterm.	82	22	1.23	30.8	15	1.59
Ternstroemia japonica Thunb.	148	21	0.42	15.8	9	1.47
Eurya japonica Thunb.	147	23	0.41	15.2	9	1.45
Myrica rubra Sieb. et Zucc.	56	20	0.99	42.2	11	1.20
Dendropanax trifidus Makino	113	23	0.37	14.4	8	1.16
Ilex goshiensis Hayata	89	26	0.60	31.7	12	1.15
Pinus luchuensis Mayr.	17	5	1.17	48.3	15	1.04
Vaccinium wrightii A. Gray	110	17	0.23	10.4	7	1.03
Tutcheria virgata Nakai	65	8	0.30	18.9	9	0.73
Symplocos prunifolia Sieb. et Zucc.	36	13	0.52	27.6	13	0.69
Diospyros morrisiana Hance	47	17	0.38	29.7	14	0.66
Randia canthioides Champ. ex Benth.	74	15	0.11	7.1	7	0.65
Diplospora dubia Masam.	55	20	0.16	12.0	8	0.55
Neolitsea aciculata Koidz.	45	15	0.20	18.8	9	0.51
Rhododendron tashiroi Maxim.	50	17	0.13	11.4	7	0.49
Camelia japonica L.	40	12	0.21	23.8	9	0.48
Ilex integra Thunb.	40	7	0.20	19.3	12	0.46
Styrax japonicus Sieb. et Zucc.	32	6	0.25	21.8	18	0.44
Quercus miyagii Koidz.	13	5	0.39	40.2	13	0.41
Symplocos lucida Sieb. et Zucc.	36	15	0.15	14.8	9	0.39
Symplocos confusa Brand	21	14	0.26	34.0	13	0.36
Cleyera japonica Thunb.	22	7	0.22	23.9	9	0.34
Rhus succedanea L.	24	12	0.20	16.3	11	0.34
Lithocarpus edulis Rehd.	20	4	0.22	23.5	15	0.33
Ilex maximowicziana Loesn.	26	15	0.10	16.9	10	0.28
Camellia sasanqua Thunb.	27	12	0.06	8.0	8	0.26
Symplocos microcalyx Hayata	29	13	0.03	5.9	6	0.25
Gardenia jasminoides Ellis	23	11	0.08	15.6	8	0.24
Rhaphiolepis indica Lindl.ex Ker.	19	2	0.10	12.8	8	0.22
Meliosma simplicifolia Roxb.	17	6	0.08	16.2	10	0.20
Remaining species (38)	157		0.93			1.93

Within a total of 80 species, only two species, *C. sieboldii* and *S. wallichii*, were encountered in all sampled plots; 22 species (27.5%) occurred only once in all thirty sampled plots (Table 1). *C. sieboldii* had the highest importance value (37.3% ranging from 26.1% to 54.9%), almost 3.6 times that of *S. wallichii* which had the second highest importance value (10.3 % ranging from 2.0 % to 25.2 %). *C. sieboldii* thus ranks as the dominant species of this subtropical forest in Okinawa.

Tree species richness (DBH ≧ 3.0 cm) was 27 per plot; the species richness index averaged 4.72 ranging from 3.91 to 5.17; diversity index 3.63 from 2.69 to 4.09 and equitability index 0.71 from 0.57 to 0.82.

The relationships between dominant species and diversity indices were examined by simple linear regression. The result showed that species diversity indices appeared obviously declined with the increase in importance value of the dominant ($r = -0.880$ for H'; $r = -0.935$ for J' and $r = -0.511$ for S'). Species richness was significantly and negatively related to the relative density of *C. sieboldii*, but not related to the relative basal area of this dominant.

Table 2. Family importance values for the 15 ecologically most important families in Okinawan subtropical forest

Family	Number of stem	Basal area (m^2)	Number of species	FIV (%)
Fagaceae	1500	31.73	3	76.3
Theaceae	894	10.04	9	40.7
Lauraceae	287	2.36	6	15.6
Aquifoliaceae	392	1.85	5	15.2
Myrsinaceae	579	1.55	3	15.1
Symplocaceae	138	1.10	8	13.8
Daphniphyllaceae	471	2.68	1	12.7
Hamamelidaceae	339	3.32	1	11.6
Elaeocarpaceae	369	1.54	2	10.6
Rubiaceae	167	0.39	5	9.4
Araliaceae	229	1.52	2	8.4
Sabiaceae	177	1.03	3	8.1
Myrtaceae	360	0.76	1	8.0
Rosaceae	175	0.70	3	7.5
Ericaceae	161	0.37	3	6.8
Other families (16)	243	3.32	25	40.1
Total (31 families)	6481	64.26	80	300

Soil chemical properties

The soils in study site had a thin A horizon, usually less than 10 cm thick, and were quite acidic with an average pH of 4.27 ranging from 3.76 to 4.66. Soil nutrients are summarized in Table 3. The dominant exchangeable cations were Al^{3+}, Ca^{2+} and Mg^{2+}, particularly Al^{3+} that alone made up 61.6% of the total exchangeable cations. The cations analyzed differed in their vertical concentration gradients: Na^+ and Al^{3+} changed little down the profile, but K^+ and Mg^{2+} were markedly concentrated toward the top. Exchangeable K^+ and Ca^{2+} in the surface soil horizons were the most variable properties with a coefficient of variation of 99.6% and 63.8%, respectively. Furthermore, more than half of the stands sampled had exchangeable K^+ values lower than 0.20 cmol (+) kg^{-1}. However, soil total N and avail-

able P concentrations were somewhat high, especially for A horizons. Most of the soils sampled had rather high values for organic C (mean value, 11.0%) in the top horizons.

Table 3. Soil chemical properties with standard errors for Okinawan subtropical forest.

Horizon	Depth (cm)	pH (H_2O)	Org-C (%)	TN (%)	Avail-P (mg kg^{-1})	Exchangeable bases (cmol (+) kg^{-1}) K^+	Ca^{2+}	Mg^{2+}	Na^+	Al^{3+}
A Mean	5.1	4.27	11.0	0.51	84.59	0.33	2.55	1.63	0.55	8.13
S.E..	2.7	0.22	2.21	0.13	28.76	0.32	1.63	0.86	0.22	1.81
B_1 Mean	22.6	4.45	2.36	0.12	35.20	0.08	0.96	0.46	0.34	6.92
S.E..	6.3	0.24	0.63	0.04	15.08	0.07	0.79	0.14	0.26	2.54
B_2 Mean	43.8	4.66	1.13	0.06	6.30	0.05	0.65	0.49	0.38	6.25
S.E..	7.2	0.13	0.31	0.02	4.29	0.07	0.47	0.17	0.29	3.04

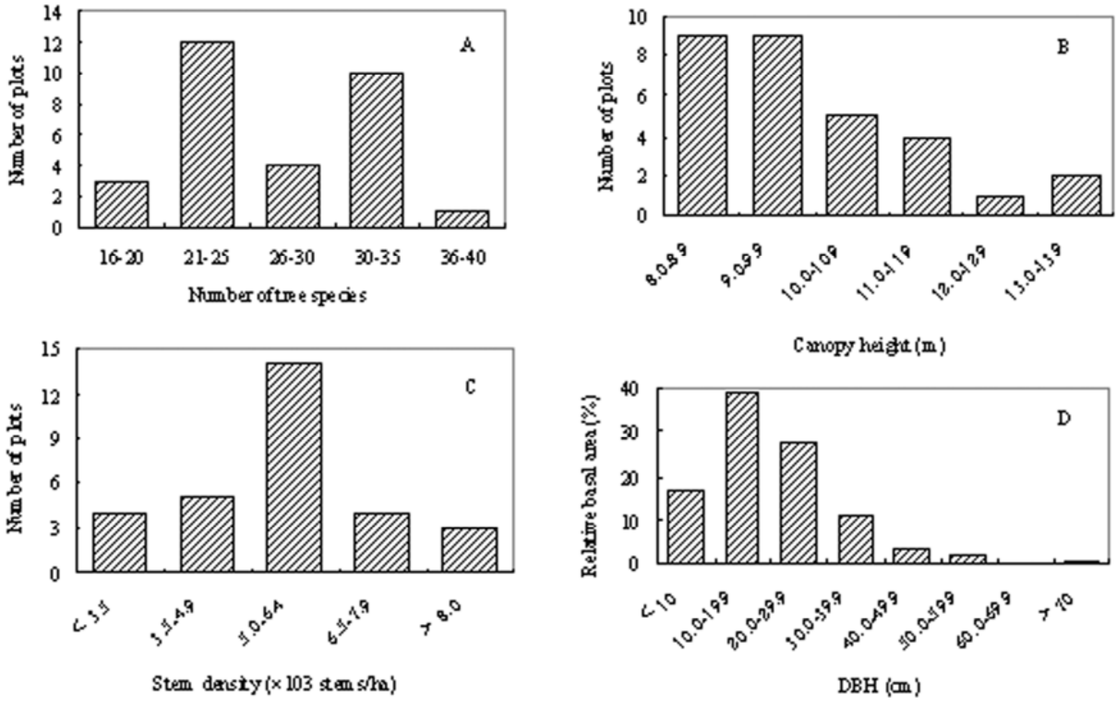

Fig. 1 Distribution of plots by (A) number of tree species; (B) mean canopy height; (C) stem density; and (D) distribution of basal area by diameter class for thirty sampling plots in Okinawan forest.

Discussion

Forest structure

Importance values indicate that Okinawan subtropical evergreen broad-leaved forest is dominated by relatively few species. *C. sieboldii* is the dominant species, which comprises 37.3% of the total importance value (Table 1). This value is similar to the dominant species in warm temperate evergreen broad-leaved forests in the mainland of Japan (Iehara et al. 1983; Takyu and Ohsawa 1997), and is high in comparison to the subtropical evergreen forests in Taiwan (Hara et al. 1997) and tropical rainforests in Amazon (Mori et al. 1983; Milliken 1998).

Another structural characteristics of the Okinawan subtropical forest is a dense and relatively low overstory canopy. The mean stem density for trees over 3.0 cm DBH was 5400 stems·ha^{-1}, and the stems less than 10 cm DBH contributed 64%. Those values are rather higher than the other evergreen broad-leaved forests of warm, humid climate in the world (e.g. Zhang et al. 1989; Lu et al. 1995; Santa Regina et al. 2001; Lan et al. 2008). Furthermore, the Okinawan evergreen broad-leaved forest has a canopy height usually lower than 15 m. Such a great density and a low canopy in our site may be attributed to persistent strong monsoon winds and frequent typhoon disturbance (Telewski 1995), and/or to soil properties, such as strong acidity and shortage of P and K (Grubb 1977).

Tree species diversity

The 80 tree species, from 31 families, recorded in this study reflect the high tree species diversity of Okinawan subtropical evergreen broad-leaved forests (Fig. 2). One recent study byYasuda et al. (1999) recorded 69 tree species of (≧ 3.0 cm DBH) within a 1-ha square plot. Another study by Hirata et al. (1991) recorded a higher diversity of more than 40 tree species (the

highest number was 47; ≧ 3.0 cm DBH) in a 20 m×20 m plot. Itow (1988) reported a strong relationship between species diversity index and warmth index along the eastern humid zone of Asia from tropical (Malay Peninsula) to warm-temperate zone (Kyushu, Japan). The more energy available, the more species are able to coexist, hence species richness and species equitability increase. Our site, located in the warmest southern-most Japan, has high species diversity (Kira 1991; Itô 1997; Hirata 1998).

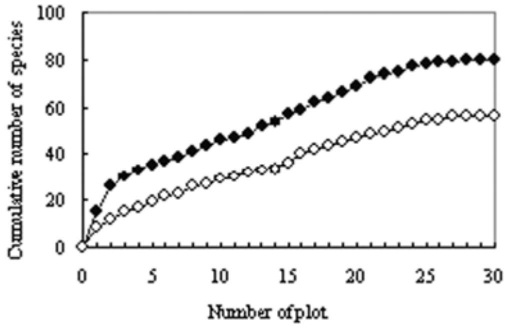

Fig. 2 Species-area curve for tree species (≧3.0 cm; ●) and canopy species (○) in Okinawan forest. Data are from thirty 20×20 m plots.

Structure and species diversity in relation to soil properties

Nutrient levels in Okinawan subtropical forest are indicative of a soil with relatively low fertility. Exchangeable K^+ and Mg^{2+} (mean values, 0.34 and 1.63 cmol (+) kg^{-1} for the surface mineral soil horizons, respectively) are within the ranges in nutrients found in Costa Rican tropical rainforest soils (Huston 1980), and another tropical rainforest soils in northeastern Australia (Brasell et al. 1980). Mean concentrations of exchangeable Ca^{2+} and available P in Okinawa are low compared to levels in Costa Rica and northeastern Australia. Comparably low levels of nutrients to our site have been reported by Stark (1971) for Amazonian rainforests and by Proctor et al. (1983) in Southeast Asia.

On the other hand, levels of organic carbon seem rather high in the top soils (the mean value reached 11.0% ranging from 5.8 % to 15.5 %). The mean concentration of exchangeable Al^{3+} for the surface soil horizons is 8.20 cmol (+) kg^{-1}, which is much and structure of thhigher than the other exchangeable cations, and could be toxic (Whitmore 1984). In addition, exchangeable Al^{3+} is an important determinant of making phosphorus insoluble in soil (Whitmore 1984). Our data showed that the available P was significantly and negatively correlated to exchangeable Al^{3+} ($R^2 = 0.415$; $p = 0.00012$; Fig. 3).

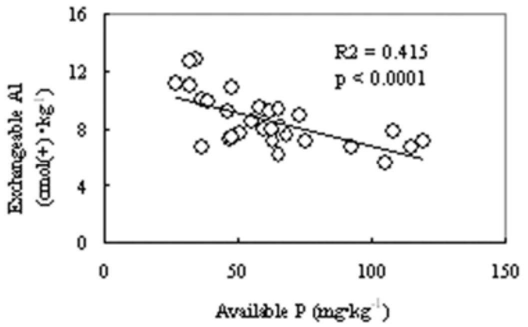

Fig. 3 Relationship between available P and exchangeable Al of the surface mineral soils in Okinawan subtropical forest.

Analysis of scatter plots and Pearson correlation coefficients (Table 4) indicates that there is no significant relationship between basal area and any individual soil chemical properties. However, there is a negatively significant relationship between stand density and soil pH ($p = 0.023$). The dominant tree height is positively correlated to soil pH ($p<0.001$), and is negatively correlated to exchangeable Al^{3+} ($p<0.001$). Our finding is in agreement with the result from Grubb (1977) that extreme acidity of soil is the primary factor for inhibiting forest growth. The species diversity index has positively significant correlations with exchangeable K^+, Ca^{2+} and Ca^{2+}/Al^{3+} ratio; and has negative correlations with organic C, total N, available P and exchangeable Al^{3+}. Therefore, compositional and structural differences within the Okinawan subtropical forest were significantly correlated to spatial variation in soil properties, indicating that soil properties may have a substantial influence on the composition is subtropical forest.

Table 4. Pearson correlation coefficients between diversity indeces, logarithmically transformed structure parameters and soil chemical properties in Okinawan subtropical forest. N = 30. Significant levels were: *, p < 0.05; **, p < 0.01; ***, p < 0.001.

	pH	Org-C	TN	Avail-P	K	Ca	Mg	Na	Al	Ca/Al
H’	0.317	-0.368*	-0.383*	-0.394*	0.573***	0.591***	-0.141	0.321	-0.452**	0.609***
J’	0.322	- 0.227	- 0.306	-0.489**	0.515**	0.571***	-0.033	0.225	-0.536**	0.593***
S’	0.257	-0.383*	- 0.350	- 0.219	0.454**	0.449**	-0.189	0.222	- 0.300	0.464**
BA	0.030	- 0.048	- 0.180	- 0.154	0.235	0.257	-0.020	0.179	- 0.073	0.240
Density	0.390*	0.053	0.301	0.126	- 0.101	0.029	0.021	0.061	- 0.278	0.088
D_{mean}	0.355	- 0.297	- 0.017	- 0.028	0.054	0.090	-0.215	0.197	- 0.253	0.133
H_{mean}	-0.413**	0.341	0.286	0.088	- 0.038	- 0.08	0.285	-0.141	0.277	- 0.122
H_D	0.707***	- 0.280	0.029	0.034	0.076	0.227	-0.011	0.201	-0.538**	0.365*

H’: Diversity index; J’: Equitability index; S’: Species richness index; BA: Basal area; D_{mean}: Mean DBH; H_{mean}: Mean height; H_D: Dominant tree height

In conclusion, the subtropical evergreen broad-leaved forest in Okinawa is species-rich, with high-density and small-statured forest structure, where few large emergents and many small-stemmed individuals are present. Such a structural character may be controlled by soil chemical properties, particularly soil pH and exchangeable Al^{3+}.

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